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The development of the embryo-sac of Arisaema triphyllum

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(WITH PLATES 13 AND 14)

The development of the embryo-sac of *Arisaema triphyllum* was first studied by Strasburger (1) in 1879, and later by Mottier (2), who published his observations in 1892. Campbell (3, 4) in his studies on the Araceae has referred to the findings of Mottier and used them as a basis for comparison. Gow (5), in his introduction to the study of the embryogeny of *Arisaema triphyllum*, reviewed the development of the embryo-sac, confirmed the findings of the second study mentioned above, and added observations of the division of a primary archesporial cell to form embryo-sac initials. The writer has been able, after the examination of several hundred ovules, to verify most of the stages in the embryo-sac development as set forth in the above-mentioned articles; but has found some notable points of difference touching the formation of megaspores from the primary archesporial cell. On the other hand the writer has found that in some respects the development of *Arisaema triphyllum* agrees very closely with that of *Symplocarpus foetidus* as shown by Rosendahl (6) in 1909.

The material for the present study was collected in proper season through four years, 1909–12. The various stages were secured from as many habitat conditions as possible. All fixing was done in the field or immediately after the return to the laboratory. Parts of young spikes and separate pistillate flowers of older spikes were fixed, some in strong chrome-acetic acid mixture, and others in chrome-osmic-acetic acid mixture, for 24–30 hours, then washed in running water for 24 hours, and finally gradually dehydrated. The blackening from osmic acid was in some cases removed by treatment of the whole specimens with hydrogen peroxide; but this resulted in considerable shrinkage, so that the specimens were of very little value. The sections were stained with safranin-gentian violet-orange G, with occasional special staining of cell walls with Bismarck brown.

OVULE AND MEGASPORE MOTHER CELL

The ovules occur in groups of two to six arising from the basal placenta in each ovary. As it first appears, each ovule is a rounded conical mass of cells covered by a clearly marked epidermal layer, but otherwise undifferentiated (FIG. 4). Soon after the ovule has reached the stage shown in FIG. 4, or about the time of the appearance of the inner integument, the primary archesporial cell, or megaspore mother cell or cells, may be found at the apex of the nucellus beneath the epidermis. These cells are hypodermal in origin, and are clearly differentiated from surrounding cells by their greater size, denser cytoplasm, and larger nuclei. The time of the differentiation of the sporogenous cells is only approximately the same as that of the development of the first integument as will be seen by a comparison of FIG. 1, 2, 3, 6, 8. FIG. 1 and 2 show two and three clearly differentiated megaspore mother cells, and FIG. 6 one such cell with complete periclinal divisions of the epidermal cells, while the integument in each of these ovules shows less growth than in FIG. 3 where no such cell can be with certainty distinguished. From one to four megaspore mother cells have been observed in a single nucellus (FIG. 1, 7, 8, 9, 11). These are usually in the hypodermal layer at first, although in a few instances some were beneath that (FIG. 2, 11, 19). The cells in FIG. 11 and 19 have been removed from the surface by periclinal division of epidermal cells. In every specimen examined the megaspore mother cells were contiguous, but in no case was there found direct evidence that they had been formed by a division of a primary archesporial cell as suggested by Mottier (2, p. 259), and by Gow (5, p. 40). The position of the cells in FIG. 19 and of the two cells at the left in FIG. 11 indicates that such an origin is possible; but the failure to find other than very rare cases of nuclear activity in cells which have not arisen by the division of epidermal cells discredits the probability of such an origin. The only form of nuclear activity found in clearly differentiated sporogenous cells was the synaptic or later stages in the tetrad division. The fact that in different ovules showing the same general structure, more than one megaspore mother cell may be found, suggests the origin of such multiple sporogenous cells by simultaneous differentiation from hypodermal cells (see FIG. 1, 2, 8). That the division of a primary archesporial cell to form two or more megaspore mother cells or embryo-sac initials is not universal, or even regular, is proven by the presence of many ovules showing the development of but one tetrad of potential megaspores or but one embryo-sac, without evidence of other crushed or damaged initial cells (FIG. 17, 18, 22, 23, 24). Fig. 7, 9, 13 show cross sections of the nucellus with the megaspore mother cells variously arranged.

THE TETRAD OF MEGASPORES

As the inner integument grows and incloses the nucellus, and the outer integument appears, the megaspore mother cells increase in size, and the epidermal cells of the nucellus undergo periclinal division. This periclinal division, shown at its beginning in FIG. 2 and 5, takes place more rapidly at the apex, sometimes forming a layer of four cells above the megaspore initials (FIG. 16, 18, 22). The division of lateral cells is also irregular and results in a final covering one to three layers of cells in thickness (FIG. 10, 11, 24). During these changes in the size and form of the ovule, the megaspore mother cells increase rapidly in size, becoming somewhat broader and much longer than the surrounding cells. Nuclear changes are also evident, and by the time the outer integument is well started most of the nuclei of the megaspore mother cells show either synapsis or closely related conditions preparatory to the first tetrad division (FIG. 7, 9, 12, 14, 16). The first division of the megaspore mother cell nucleus is quickly followed by the second, the result being a tetrad of potential megaspores (FIG. 18). The first division is usually followed by the formation of a cell wall as in FIG. 22 and 24, but this is not always the case, as is shown in FIG. 23. These divisions are usually transverse as shown in the cell at the left in FIG. 16, in the middle cell of FIG. 15*a*, and in FIG. 24. The resulting megaspores usually lie in a row parallel to the long axis of the nucellus (FIG. 18). That the first division may be longitudinal is shown by preparations similar to that in FIG. 10, and that the later divisions may vary from a transverse direction is shown in the upper cell in FIG. 22. From such divisions we might expect the formation of two parallel rows of two megaspores each, or a row of two parallel to the long axis of the nucellus with another transverse pair, as described for *Symplo-*

carpus foetidus by Rosendahl (6, p. 3). Where more than one megaspore mother cell is in a nucellus, division of all the nuclei proceeds regularly and may or may not be simultaneous. The most nearly simultaneous cases found are shown in FIG. 9, 19, 19*a*. Finally, limited space probably causes a crowding in such cases, which results in the checking of activity in some cells and their destruction by the growth of others, as suggested by the cells at the left in FIG. 15, 15*a*.

A few preparations show a cell in a position to indicate its origin as a tapetal cell (FIG. 17*t*). The same possibility is suggested by Gow (5, p. 39–40), in FIG. 6, and is also mentioned by Campbell (3, p. 7) for *Dieffenbachia Seguine*. Such a tapetal structure is shown to be well developed normally in *Symplocarpus foetidus* by Rosendahl (6, p. 2, *pl. 1. f. 4* and *pl. 3. f. 31*). The finding of but one such cell showing disorganization as the megaspores develop seems to the writer sufficient evidence to justify the conclusion that the formation of a functional tapetum in *Arisaema triphyllum* is unusual or even questionable.

As has been stated above, during the enlargement and divisions of the megaspore mother cells, the outer cells of the nucellus undergo periclinal divisions until the sporogenous cells appear quite deeply seated. During the same time the nucellar cells become well filled with starch (FIG. 15 and 17). As a result of the later gametophyte growth, the lateral portion of the nucellus with its contained food material is consumed, so that the mature embryo-sac is in contact with the inner integument, except at the apex, where a cap of nucellar cells persists (FIG. 20 and 21). The temporary storage of food where it is so readily available for use by the growing embryo-sac may account for the rapid development of the latter as given below.

THE EMBRYO-SAC

One of the megaspores develops into the embryo-sac at the expense of the others and of the nucellar tissue. Three nuclear divisions occur in rapid succession as in *Symplocarpus foetidus* (6, p. 3). The short time required for these divisions is indicated by the fact that out of many preparations of material gathered at one time, and showing about this stage, but very few show anything between the first nuclear division of the megaspore (FIG. 20) and the mature embryo-sac (FIG. 20). The daughter nuclei of the first division remain centrally located in the cell until after the second division (FIG. 26). Later a normal egg cell and two synergidae are formed close in the apex of the embryo-sac, and in some cases three antipodals are present (FIG. 20). The antipodal cells are poorly developed however, only occasionally showing typical angiosperm structure, and never showing the remarkable development described by Campbell (3, p. 11) and Rosendahl (6, p. 5) for other members of the Araceae. As far as the writer has been able to determine, the polar nuclei show no such fusion as described by Gow (5, p. 41), but remain separate as in *Anthurium* (3, p. 15). In every case where a polar nucleus was observed after fertilization of the egg, the lower one was found separate, greatly enlarged, and often disintegrating near the antipodals. Further details concerning the fate of the polar nuclei and of the antipodal structure will be more fully dealt with in a subsequent paper.

Where more than one tetrad of potential megaspores are formed in one nucellus, the usual course of events is for some one cell from one tetrad to germinate while the other spores are crushed or broken down. In rare cases more than one embryo-sac have been found developing in the same nucellus. In one ovule two well-developed embryo-sacs were found side by side and of approximately the same size, but unfortunately one lay directly beneath the other in the section. The only preparation showing two such structures in the same section is shown in FIG. 21. These present a marked difference in size as well as deficiencies in antipodal structure. As stated above, such imperfect development of antipodals is not rare in otherwise normal embryo-sacs.

SUMMARY

The present study has verified most of the findings of other investigators, but has given results at variance with their reports in regard to the following points.

(*a*) The origin of the several megaspore mother cells from a single primary archesporial cell is doubtful.

The first division in the formation of the tetrad has been probably mistaken by earlier investigators for a division of a primary archesporial cell into embryo-sac initials.

(*b*) The formation of a tetrad of potential megaspores from some of which the embryo-sac or sacs develop, instead of from an archesporial cell, is shown.

(*c*) More than one embryo-sac may be developed in *Arisaema triphyllum*, as Campbell (4, p. 671) has shown for other members of the Araceae.

(*d*) The fusion of the polar nuclei is doubtful.

(*e*) The antipodal cells rarely develop fully as in typical angiosperms.

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Description of plates 13 and 14

All drawings were made with the aid of a camera lucida.

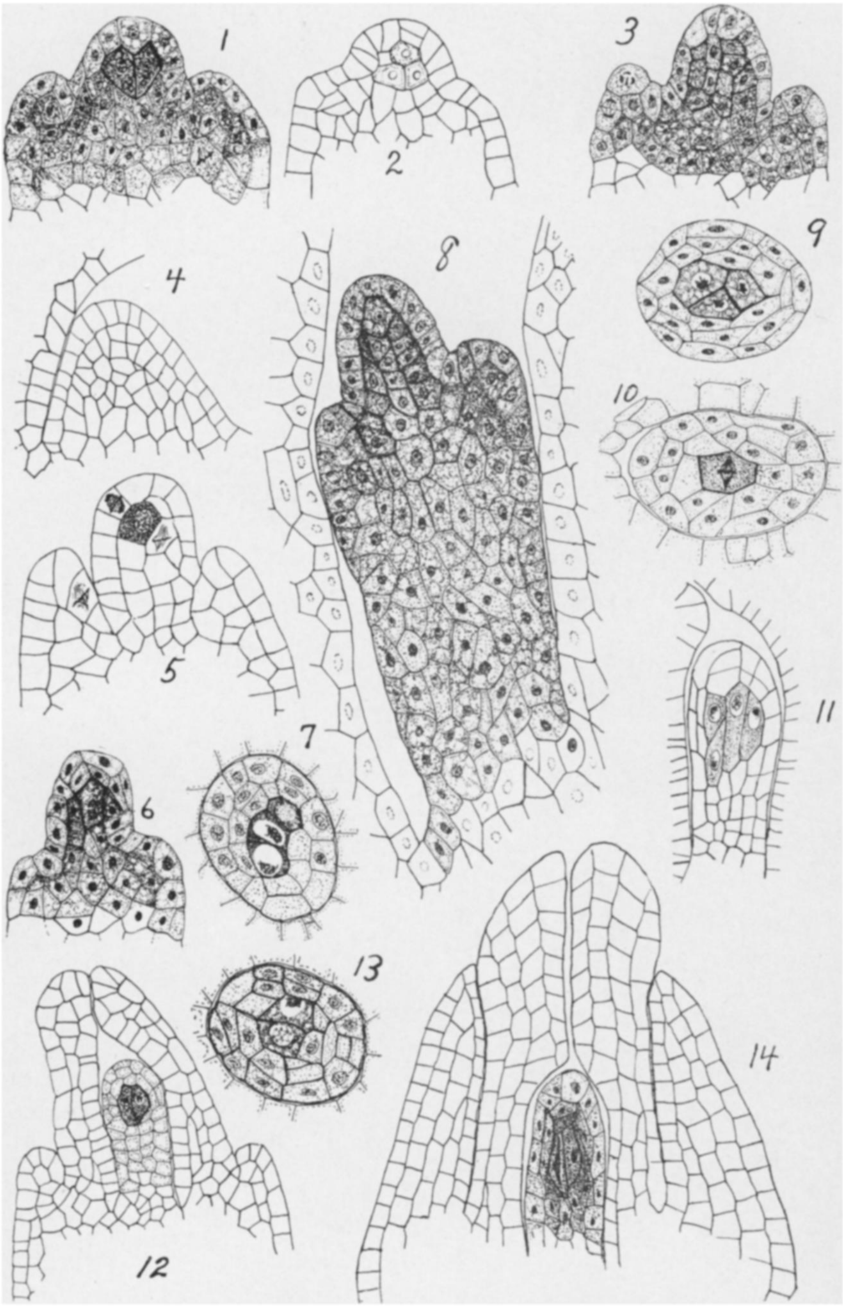
FIG. 1. Longitudinal section of a young ovule with two megaspore mother cells in normal position shortly after the beginning of differentiation. ×225.

FIG. 2. Longitudinal section of young ovule with three sporogenous cells differentiated. The two lower cells may be considered as lateral hypodermal cells. ×225.

FIG. 3. Longitudinal section of ovule slightly larger and older than those shown in FIG. 1 and 2, but without any clearly differentiated sporogenous cells. ×225.

FIG. 4. Longitudinal section of very young ovule before differentiation of sporogenous cells and beginning of integuments. ×335.

FIG. 5. Longitudinal section of ovule showing lateral megaspore mother cell, a possible tapetal cell at the right, and the beginning of periclinal division of epidermal cells. ×225.



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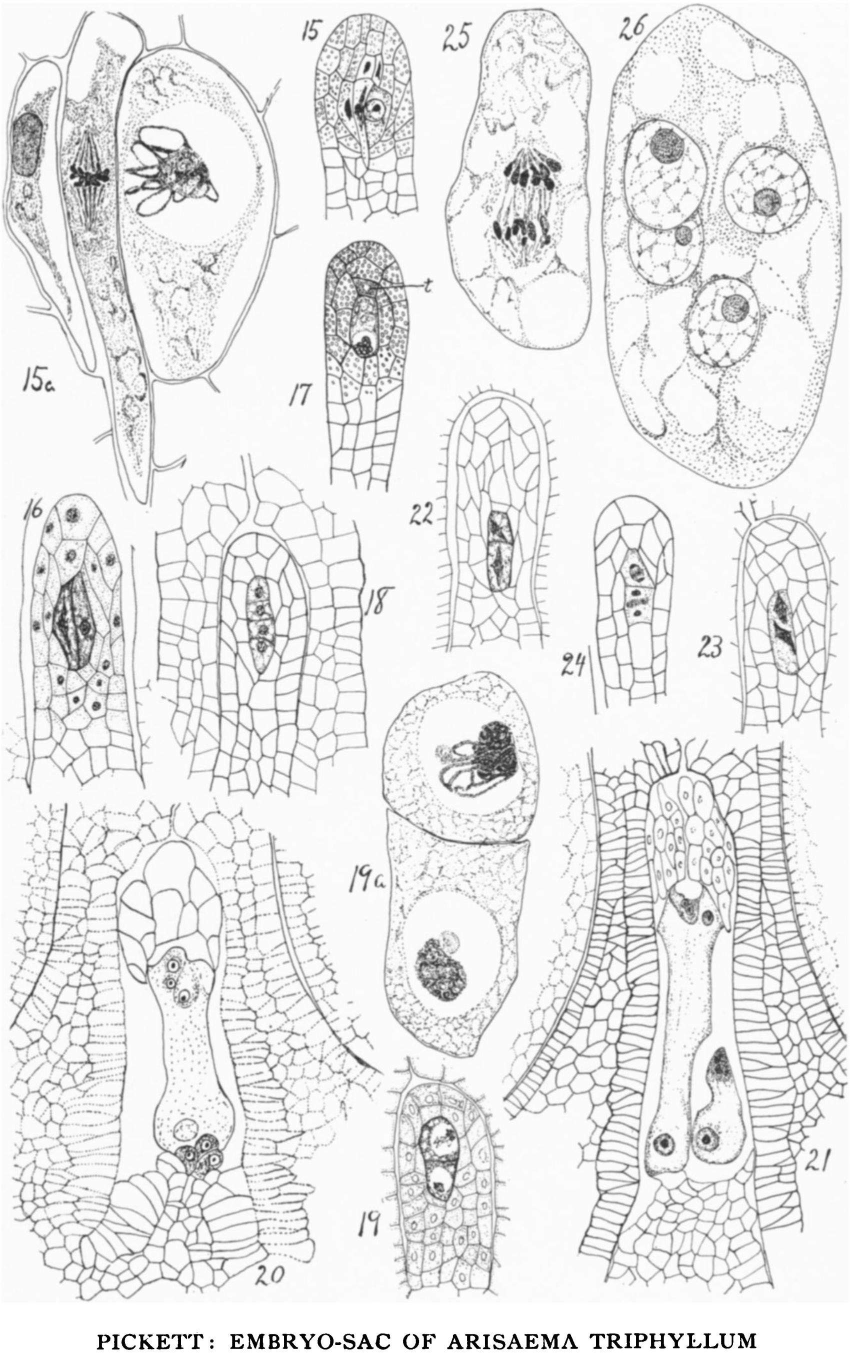

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FIG. 6. Longitudinal section of ovule showing one megaspore mother cell and completed periclinal division of epidermal cells. ×225.

FIG. 7. Cross section of nucellus showing layer of 2 to 3 cells surrounding three megaspore mother cells. ×335.

FIG. 8. Longitudinal section of the whole ovule and part of ovary walls. ×225.

FIG. 9. Cross section of nucellus similar to FIG. 7, but showing different arrangement of megaspore mother cells. This shows very nearly simultaneous preparation for nuclear division. ×335.

FIG. 10. Cross section of nucellus showing the spindle of a longitudinal first division of a megaspore mother cell. ×335.

FIG. 11. Longitudinal section of nucellus with four megaspore mother cells. The position of the two at the left suggests a possible origin from a common archesporial cell. ×225.

FIG. 12. Longitudinal section of ovule to show the development of the integuments at the time of preparation for first tetrad division. ×125.

FIG. 13. Cross section of nucellus to show irregularity of periclinal division of outer cells. ×335.

FIG. 14. Longitudinal section of ovule to show the development of integuments at the time of the first tetrad division. ×125. (See FIG. 16.)

FIG. 15. Longitudinal section of nucellus showing some sporogenous cells crushed by the growth of others. ×250.

FIG. 15*a*. Sporogenous cells of FIG. 15. ×830.

FIG. 16. Higher magnification of the nucellus shown in FIG. 14. ×250.

FIG. 17. Longitudinal section of nucellus showing a possible tapetal cell, *t*. ×250.

FIG. 18. Longitudinal section of nucellus showing a row of four potential megaspores. ×250.

FIG. 19. Longitudinal section of nucellus showing two megaspore mother cells, one below the other. ×250.

FIG. 19*a*. Sporogenous cells of FIG. 19. ×830. The nuclei are in synapsis.

FIG. 20. Longitudinal section of ovule with one mature embryo-sac. ×160.

FIG. 21. Longitudinal section of ovule with two embryo-sacs. ×160.

FIG. 22. Longitudinal section of nucellus showing the second tetrad division and the wall formed after the first division. This shows the sporogenous cells buried unusually deep. ×250.

FIG. 23. Same as FIG. 22, but without any cell wall after the first division. ×250.

FIG. 24. A later stage than in FIG. 22. ×250.

FIG. 25. Section of a megaspore showing the first nuclear division. ×830.

FIG. 26. Section showing four nuclear stage in the development of the embryo-sac. ×830.